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RESEARCH PAPER

Interaction of a bioherbicide and glyphosate for controlling hemp sesbania in glyphosate-resistant soybean

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The bioherbicidal fungus, *Colletotrichum truncatum* (Schwein.) Andrus & Moore, was tested at different inoculum concentrations alone and in combination with, prior to or following treatment with different rates of glyphosate (*N*-[phosphonomethyl]glycine) (Roundup Ultra) for the control of hemp sesbania (*Sesbania exaltata* [Raf.] Rydb. ex A.W. Hill) in Roundup Ready soybean field plots. *Colletotrichum truncatum* and glyphosate were applied in all pair-wise combinations of 0, 1.25, 2.5, 5.0, and 10.0×10^6 spores mL^{-1} (i.e. 3.125, 6.25, 12.5, and 25×10^{11} spores ha^{-1}), and 0.15, 0.30, 0.60, and 1.2 kg ha^{-1}, respectively. Weed control and disease incidence were enhanced at the two lowest fungal and herbicidal rates when the fungal spores were applied after glyphosate treatment. The application of the fungus in combination with or prior to glyphosate application at 0.30 kg ha^{-1} resulted in reduced disease incidence and weed control regardless of the inoculum's concentration. At the highest glyphosate rates, the weeds were controlled by the herbicide alone. These results suggest that it might be possible to utilize additive or synergistic herbicide and pathogen interactions to enhance hemp sesbania control.

Keywords: biocontrol agent, bioherbicide, *Colletotrichum truncatum*, glyphosate, synergistic interaction.

INTRODUCTION

The use of fungi and bacteria as inundative biological control agents (bioherbicides) has been recognized as a significant technological alternative to chemical herbicides (Rosskopf *et al*. 1999; Boyette 2000; Charudattan 2001, 2005; Hoagland 2001). Considerable interest exists worldwide in this field, with active scientific research and commercial development underway in the USA, Canada, Europe, Australia, Japan, and other countries (Charudattan 2001, 2005). Previous research has indicated that the fungus, *Colletotrichum truncatum*, is an effective bioherbicide for controlling hemp sesbania (*Sesbania exaltata* [Raf.] Rydb. ex A. W. Hill) (Boyette 1991; Boyette *et al*. 1993; Abbas & Boyette 2000), one of the 10 most troublesome weeds in three southern states in the USA: Arkansas, Louisiana, and Mississippi (Dowler 1997). Ninety percent of the weeds were controlled and the control levels were similar to those achieved with the herbicide acifluorfen {5-(2-chloro-4-[trifluoromethyl] phenoxy)-2-nitrobenzoic acid} (Boyette *et al*. 1993). In those studies, test plots were conducted in "conventional", non-genetically modified soybeans ("Centennial" cv.). Since the mid-to-late 1990s, genetically modified crops, such as soybean, have replaced many "conventional" varieties (Duke 1996). Glyphosate (*N*-[phosphonomethyl]glycine; trade name: Roundup Ultra) is a broad-spectrum, systemic herbicide that can be applied over the top (postemergence) to glyphosate-resistant soybean varieties (Roundup Ready). In most cases, the use of glyphosate on glyphosate-resistant soybean reduces the need for pre-emergence herbicides and other postemergence herbicides. It is estimated that, currently, ~85–90% of soybean produced in the delta region of the south-eastern USA are Roundup Ready

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varieties (Anonymous 2005). As a result of the prevalent usage of glyphosate in Roundup Ready soybean, it was important to determine if bioherbicides, such as *C. truncatum*, could be used in conjunction with, or in combination with, glyphosate at the recommended or reduced glyphosate application rates.

Christy *et al.* (1993) reported a synergy between several different herbicides and fungal plant pathogens. For example, the trimethylsulfonium salt of glyphosate was found to synergize *Xanthomonas campestris* against several weed species, presumably related to interference with the weeds' ability to produce phytoalexins derived from the shikimate pathway. Other synergistic interactions involving herbicides and plant growth regulators and bioherbicidal fungal pathogens have been discovered and some were granted patents in the USA (Caulder & Stowell 1988a,b). In later studies, the herbicides, acifluorfen and bentazon (3-[1-methylethyl]-[1*H*]-2,1,3-benzothiadiazin-4[3*H*]-one 2,2-dioxide), were the most effective synergists and provided increased control in several weed : pathogen combinations: sicklepod (*Senna obtusifolia*, formerly *Cassia obtusifolia* [L.] Irwin & Barneby) and *Alternaria cassiae* Jurair & Khan; northern jointvetch (*Aeschynomene virginica* [L.] Britton, Sterns & Poggenb.) and *Colletotrichum gloesporioides*; hemp sesbania and *C. truncatum*; and Florida beggarweed (*Desmodium tortuosum* [SW.] DC.) and *Fusarium lateritium* Nees. Wymore *et al.* (1987) reported that co-applications of *Colletotrichum coccodes* Wallr. and the herbicide, thidiazuron, to velvetleaf (*Abutilon theophrasti* Medic.) increased pathogen infection and weed control compared with either component applied alone. Heiny (1994) found that *Phoma proboscis* Heiny, at 10^7 spores mL^{-1} applied with 2,4-D ([2,4-dichlorophenoxy]acetic acid) plus MCPP (2-[4-chloro-2-methylphenoxy]propanoic acid) at sublethal rates, controlled field bindweed (*Convolvulus arvensis* L.) more effectively than the herbicide mixture alone and as effectively as the pathogen at a 10-fold higher rate. Similarly, a sublethal dose of glyphosate (50 μmol L^{-1}) suppressed the biosynthesis of a phytoalexin derived from the shikimate pathway in sicklepod infected by *Alternaria cassiae* Jurair & Khan, reducing the resistance of the weed to fungal infection and disease development (Sharon *et al.* 1992). Those studies suggested that the efficacy of bioherbicides can be enhanced through synergism with synthetic herbicides applied at rates below those recommended by the manufacturer. The objectives of the present study were to: (i) evaluate the potential synergy between *C. truncatum* and glyphosate for the control of hemp sesbania; and (ii) determine the effective application timing and rates for delivering the pathogen.

MATERIALS AND METHODS

Inoculum production and bioherbicide formulation

A single strain of *C. truncatum* (NRRL 18434; Agricultural Research Service Patent Culture Collection, Peoria, IL, USA) was used in all of the experiments. The fungus was preserved in screw-capped tubes containing sterilized soil (Bakerspigel 1953). The inoculum (spores) of *C. truncatum* was produced in 10 cm plastic Petri dishes containing potato dextrose agar (PDA; Difco Laboratories, Franklin Lakes, NJ, USA). The agar surfaces were flooded with 3 mL of a *C. truncatum* spore suspension containing 2×10^6 conidia mL^{-1}. The PDA plates were inverted on open-mesh wire shelves and incubated at 25°C for 5 days in fluorescently lighted incubators under cool–white fluorescent lighting (12 h photoperiod). The spores were harvested by rinsing the cultures with deionized distilled water and filtering through double-layered cheesecloth. The spore densities were determined with hemocytometers (Improved Neubauer model; AO Scientific, Buffalo, NY, USA) and the dilutions were made with distilled, deionized water to give the desired inoculum concentrations. Previous research has shown that the infectivity and biocontrol efficacy of *C. truncatum* is increased by an unrefined corn oil-in–water emulsion containing 0.2% (v/v) surfactant (Boyette 1994; Egley & Boyette 1995). Therefore, a 1:9 ratio of unrefined corn oil : aqueous component with surfactant was utilized in all of the treatments. The emulsion formulations were prepared by adding unrefined corn oil to aqueous fungal components and thoroughly mixing (~10 s) with a cordless, hand-held mixer (Hamilton Beach; Glen Allen, VA, USA) immediately before the field applications were made. When used, glyphosate (600 g ae L^{-1}; Roundup Ultra, Monsanto, St Louis, MO, USA) was added to the spore–emulsion formulations immediately before treatment and mixed as previously described.

Field studies and experimental design

The field plots were established in 2001 and 2002 at the Southern Weed Science Research Unit Experimental Farm, Stoneville, MS, USA, in Roundup Ready soybean test plots. The treatments consisted of glyphosate at 0, 0.15, 0.30, 0.60, and 1.2 L ha^{-1} followed by, with or prior to *C. truncatum* spores at inoculum densities of 0, 1.25, 2.5, 5.0, and 10.0×10^6 spores mL^{-1} at a volume of 250 L ha^{-1}. All of the applications were made using pressurized backpack sprayers (Gilmour, Somerset, PA, USA) when the weeds were in the second-to-fourth leaf stage of growth (~6–8 cm in height). The plots consisted

of eight 6 m rows, with the four center rows receiving treatment. The disease development and weed mortality data were recorded at 7 day intervals over a period of 21 days. A split-block experimental design was utilized, with the glyphosate rates as the main plots and the *C. truncatum* rates as the subplots. In each of the 2 years, all of the treatments were replicated four times. The data over the 2 years were averaged, followed by subjection to Bartlett's test for homogeneity of variance (Gomez & Gomez 1984). The data were analyzed using analysis of variance. The percentage data of the hemp sesbania injury/control and of the biomass reductions were subjected to arc–sin transformation prior to analysis. The treatment means and standard errors of the mean are presented.

Analyses of the treatment interactions

The interactions between the glyphosate and *C. truncatum* treatments when glyphosate was added prior to, after or together with the bioherbicide were analyzed according to Colby (1967), using the equation, $E = X_A Y_B/100$, in which X_A and Y_B represent weed control as a percentage of the control, with herbicide A (glyphosate) used at dosage p and bioherbicide B (*C. truncatum*) used at dosage q, respectively. E is the expected survival as a percentage of the control for mixture A and B at dosages p and q. The observed response was experimentally determined by comparing the activity of single components with the mixtures containing the same rate of the components applied singly. Deviation from the expected response, as calculated from the level of interaction R, that is, the ratio of the expected and the observed response of the two components, indicates synergism or antagonism. By definition (Colby 1967), additive interactions occur if $R = 1$, synergism occurs if $R > 1$, and antagonism occurs if $R < 1$. However, due to the inherent variability of a biological test system, synergism has been considered significant if $R = 1.5$ and antagonism is significant if $R = 0.5$. Additive interactions are present when R is between 0.5 and 1.5 (Gisi *et al.* 1985).

RESULTS AND DISCUSSION

In the treatments where glyphosate was applied prior to the fungal treatments, hemp sesbania was effectively controlled by *C. truncatum* alone only at high rates (10.0×10^6 spores mL^{-1}) and with glyphosate alone at 0.6 and 1.2 kg ha^{-1} (Fig. 1). However, the weeds were controlled by 85, 90, and 93%, respectively, at inoculum concentrations of 2.5, 5.0, and 10.0×10^6 spores mL^{-1}, respectively (Fig. 1). With the exception of the 1.2 kg ha^{-1} glyphosate rate, in which 100% weed control

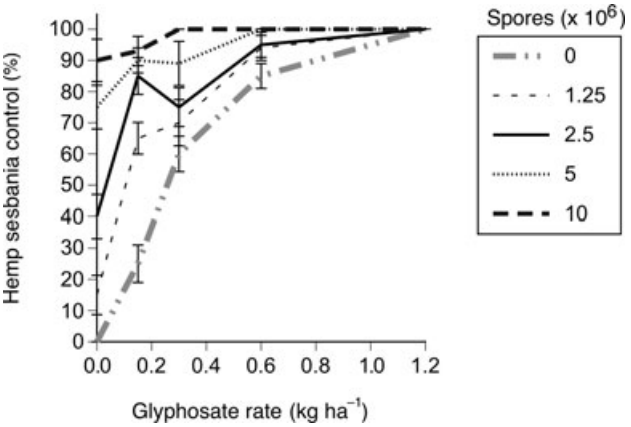

Fig. 1. Hemp sesbania control by *Colletotrichum truncatum* preceded by glyphosate. The error bars represent one standard error of the mean.

occurred, weed control was significantly improved in the plots treated with reduced glyphosate rates when the fungal component was applied, regardless of the inoculum concentration (Fig. 1). Weed control at reduced herbicide rates (0.15 and 0.30 kg ha^{-1}) was significantly improved when *C. truncatum* was applied after the glyphosate (Fig. 1). An analysis of the possible interactions of the herbicide and bioherbicide, when glyphosate was applied prior to *C. truncatum*, showed some synergistic combinations (Table 1). Synergism occurred when glyphosate at 0.15 kg ha^{-1} was applied prior to *C. truncatum* at the 1.25, 2.5, and 5.0 rates (10^6 spores mL^{-1}). An additive interaction occurred at the glyphosate rate of 0.30 kg ha^{-1} and a *C. truncatum* inoculation rate of 1.25×10^6 spores mL^{-1}. Although all the observed and expected data are presented in Tables 1–3, the R-values for the rates of spores and/or herbicide that yielded high efficacies by each component alone are not calculated as meaningful interactions cannot be determined.

In general, weed control was reduced when applications were made as tank mixtures (Fig. 2) or when the fungus was applied prior to the herbicidal treatment (Fig. 3). However, ~70% weed control was achieved at 5.0×10^6 and 10.0×10^6 spores mL^{-1} inoculum concentrations with the 0.25 kg ha^{-1} glyphosate treatment (Figs 2,3). An analysis of these results for the interactions showed that several combinations of rates of these two components gave additive or antagonistic responses (Tables 2,3), which corroborates the percentage weed control data presented in Figs 2 and 3. Although not tested here, the toxicity of glyphosate or the ingredients in its formulation could be the cause of some of the antagonistic responses found here. Glyphosate is readily metabolized or degraded by various microorganisms, but its metabo-

Table 1. Action of glyphosate applied to hemp sesbania seedlings prior to *Colletotrichum truncatum* application

Glyphosate (kg ha^{-1})	*Colletotrichum truncatum* (10^6 spores mL^{-1})	Survival (%)†		R-value: interaction‡
		Observed	Expected	
0.00	0.00	100	100	–
	1.25	85	85	–
	2.50	60	60	–
	5.00	25	25	–
	10.00	10	10	–
0.15	0.00	75	75	–
	1.25	35	64	1.80 (syn.)
	2.50	15	45	3.00 (syn.)
	5.00	10	19	1.90 (syn.)
	10.00	7	8	NS
0.30	0.00	40	40	–
	1.25	30	34	1.13 (add.)
	2.50	25	24	NS
	5.00	11	10	NS
	10.00	0	–	–
0.60	0.00	15	15	–
	1.25	6	13	NS
	2.50	5	9	NS
	5.00	0	–	–
	10.00	0	0	–
1.20	0.00	0	0	–
	1.25	0	0	–
	2.50	0	0	–
	5.00	0	0	–
	10.00	0	0	–

† Expected values were determined by $E = X_A Y_B/100$; ‡ the ratio between the expected and observed survival (R = expected/observed). add., additive interaction; NS, not significant (Gisi *et al*. 1985); syn., synergistic interaction.

lism in plants does not occur or is extremely slow (Hoagland 1996). Thus, applying glyphosate prior to pathogen application allows the absorption, translocation, and action of the herbicide (without metabolic degradation) and diminishes its possible toxicity to the living propagules of the bioherbicide.

In the present study, narrow row (51 cm) spacings were utilized, which allow the soybean crop to reach full canopy closure quickly, thereby reducing weed competition (Legere & Schreiber 1989) and increasing the yield potential (Nelson & Renner 1999). The relatively rapid canopy closure also might create a more favorable environment for the fungus to infect and kill hemp sesbania.

The interactions between various herbicides and plant pathogens (Altman *et al*. 1990; Smith 1991; Hoagland 1996), herbicide induction of microbial invasion of plant roots (Greaves & Sargent 1986), and the interactions of sublethal herbicide doses on root pathogens (Lévesque & Rahe 1992) have been reviewed. One of the earliest reports indicating that herbicides could block resistance to pathogens was the increased infection of an incompatible race of *Phytophthora megasperma* Drechs. f. sp. *glycinea* T. Kuan & D. C. Erwin in soybean, which was caused by glyphosate (Keen *et al*. 1982). Low levels of glyphosate reduced the phytoalexin, glyceollin, which was suggested as the possible operative mechanism. Other interactions of *A. cassiae* and sicklepod with glyphosate showed that glyphosate suppressed the sicklepod defense response by lowering phytoalexin (2-[*p*-hydroxyphenoxy]-5,7-dihydroxychrome) production and, thus, the herbicide acted synergistically with this pathogen (Sharon *et al*. 1992). The interactions of glyphosate and *A. cassiae* in sicklepod represent the most completely understood biochemical events associated with pathogen–herbicide interactions. Numerous other

Table 2. Interaction of glyphosate with *Colletotrichum truncatum* when applied to hemp sesbania seedlings

Glyphosate (kg ha^{-1})	*Colletotrichum truncatum* (10^6 spores mL^{-1})	Survival (%)†		R-value: interaction‡
		Observed	Expected	
0.00	0.00	–	–	–
	1.25	85	85	–
	2.50	60	60	–
	5.00	25	25	–
	10.00	10	10	–
0.15	0.00	75	75	–
	1.25	78	64	0.82 (add.)
	2.50	76	45	0.59 (add.)
	5.00	75	19	0.25 (ant.)
	10.00	70	8	0.11 (ant.)
0.30	0.00	40	40	–
	1.25	38	34	0.89 (add.)
	2.50	36	24	0.67 (add.)
	5.00	31	10	0.32 (ant.)
	10.00	30	12	0.40 (ant.)
0.60	0.00	15	15	–
	1.25	5	13	–
	2.50	4	9	–
	5.00	0	4	–
	10.00	0	3	–
1.20	0.00	0	0	–
	1.25	0	0	–
	2.50	0	0	–
	5.00	0	0	–
	10.00	0	0	–

† Expected values were determined by $E = X_A Y_B/100$; ‡ the ratio between the expected and observed survival (R = expected/observed). add., additive interaction; ant., antagonistic interaction.

examples have correlated phenylalanine ammonia-lyase (PAL) activity with pathogen challenge and plant defense (Hoagland 1999). Compounds that inhibit PAL, in most cases, have caused increased susceptibility to disease. Furthermore, several herbicides (including glyphosate) alter the levels of PAL, phytoalexins, and phenolic compounds in plants, all of which affect plant defense against pathogens (Hoagland 2000). Recently, several herbicides, including glyphosate, were tested at reduced rates for possible interactions with the fungal pathogen, *Pyriculoria setariae* Niskoda, for the control of green foxtail (*Setoria viridis* [L.] Beauv.) (Peng & Byer 2005). Propanil (*N*-[3,4-dichlorophenyl] propanamide), quinclorac (3,7-dichloro-8-quinolinecarboxylic acid), and sethoxydim {2-(1-[ethoxyimino]butyl)-5-(2-[ethylthio]propyl)-3-hydroxy-2-cyclohexen-1-one} applied ≤6 h prior to the pathogen generally resulted in greater efficacy. Only sethoxydim plus the fungus significantly increased green foxtail control compared to the herbicide or pathogen applied singly. Glyphosate and glufosinate (2-amino-4-[hydroxymethylphosphinyl]butanoic acid) appeared to work cooperatively with the pathogen. In more recent studies, glyphosate interacted synergistically with the bioherbicidal pathogen, *Myrothecium verrucaria* (Alb. & Schwein.) Ditmar: Fr., when certain rates of herbicide and bioherbicide were used to control redvine, (*Brunnichia ovata* [Walt.] Shinners) (Boyette *et al*. 2006).

The results from this research indicate that the use of sublethal rates of glyphosate has a positive effect on the biocontrol efficacy of *C. truncatum* and that the rate of both glyphosate and the pathogen can be optimized for maximum efficacy. These results also indicate that the timing of the herbicide and pathogen applications is critical. The application of glyphosate prior to the fungal applications provided the best overall weed control

Table 3. Action of *Colletotrichum truncatum* applied to hemp sesbania seedlings prior to glyphosate application

Glyphosate (kg ha^{-1})	*Colletotrichum truncatum* (10^6 spores mL^{-1})	Survival (%)†		R-value: interaction‡
		Observed	Expected	
0.00	0.00	100	100	–
	1.25	85	85	–
	2.50	60	60	–
	5.00	25	25	–
	10.00	10	10	–
0.15	0.00	75	75	–
	1.25	75	64	0.85 (add.)
	2.50	72	45	0.62 (add.)
	5.00	70	19	0.27 (ant.)
	10.00	68	8	0.12 (ant.)
0.30	0.00	40	40	–
	1.25	40	16	0.40 (ant.)
	2.50	36	14	0.39 (ant.)
	5.00	30	12	0.40 (ant.)
	10.00	28	11	0.39 (ant.)
0.60	0.00	15	15	–
	1.25	3	0	–
	2.50	2	0	–
	5.00	0	0	–
	10.00	0	0	–
1.20	0.00	0	0	–
	1.25	0	0	–
	2.50	0	0	–
	5.00	0	0	–
	10.00	0	0	–

† Expected values were determined by $E = X_A Y_B/100$; ‡ the ratio between the expected and observed survival (R = expected/observed). add., additive interaction; ant., antagonistic interaction.

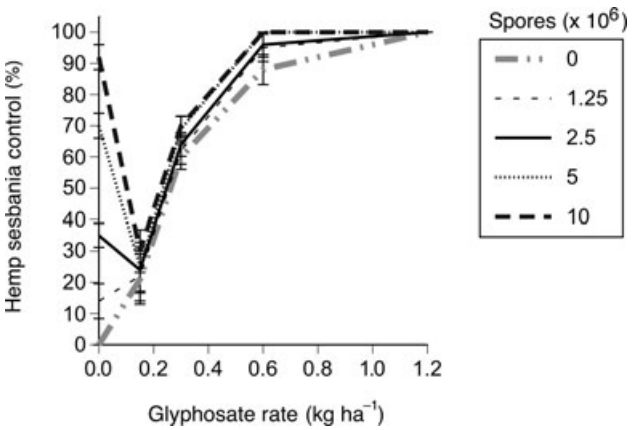

Fig. 2. Hemp sesbania control by *Colletotrichum truncatum* applied with glyphosate. The error bars represent one standard error of the mean.

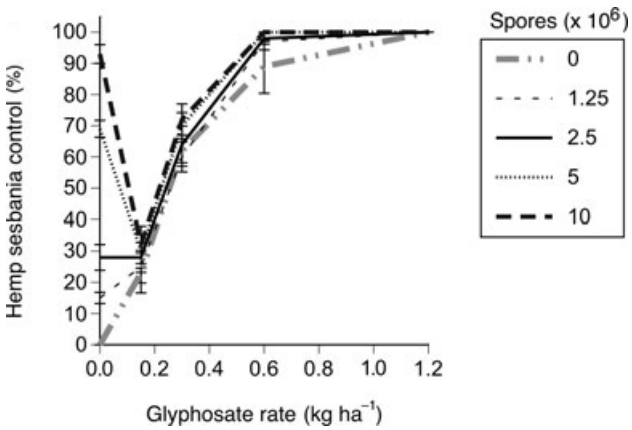

Fig. 3. Hemp sesbania control by *Colletotrichum truncatum* followed by glyphosate. The error bars represent one standard error of the mean.

efficacy at reduced pathogen rates, an effect also demonstrated in interaction studies with *M. verrucaria* on kudzu (*Pueraria lobata* [Willd.] Ohwi), trumpetcreeper (*Campsis radicans* [L.]), and redvine (Boyette *et al.* 2006). In the present study, maximal weed control was achieved when the herbicide and the pathogen were applied separately, thus requiring two passes through the field. However, it should be noted that the pathogen application occurred almost immediately after glyphosate application; thus, it might be possible to develop a mechanized spray system that would apply the herbicide and the pathogen separately. Future studies will be conducted to determine the time course effects on infectivity and weed control potential.

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